THE UNIVERSITY OF ALBERTA

The Effect of Temperature on Translocation in *Phaseolus vulgaris* L.

by

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Abstract

The purpose of this study was to determine the effect of temperature on translocation when the temperature of the whole plant is varied. *Phaseolus vulgaris* plants were simplified to single source-single sink systems. The rates of photosynthesis in the source leaves and the rates of translocation from the source leaves to the sink leaves were monitored, using a closed-loop, steady-state, $^{14}CO_2$-labelling system, as the temperature of the simplified plants was changed. The results indicate that translocation increases with temperature to approximately 25°C, where the rate of increase begins to level off. This was shown to be due to an effect of temperature on translocation, rather than to an effect of temperature on photosynthesis.

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1. Introduction

The purpose of this study was to determine the effect of temperature on translocation when the temperature of the whole plant is varied. Although many studies have been done on the effect of temperature on translocation, most of these have involved varying the temperature of only a localized part of the plant. While these studies have yielded useful information on how temperature affects each of the component parts of the translocation system, they have failed to show how varying the temperature of all the component parts would affect the functioning of the translocation system as a whole.

Only a few studies have been done on the effect of varying the temperature of the whole plant, and, in general, these have not been definitive. The results of Hewitt and Curtis (1948), who measured the loss of dry weight in leaves of plants held in darkness, are complicated by the depletion of carbohydrate reserves at high temperatures, and the results of Whittle (1964), who estimated translocation from radioactivity profiles in photosynthesising plants, are complicated by the inability to separate the effect of temperature on translocation from its effect on photosynthesis.

In order to definitively determine the effect of temperature on translocation, it was necessary to use a photosynthesising plant, and to account for the possible indirect effect of temperature on translocation, through its

effect on photosynthesis. This was done using *Phaseolus vulgaris* plants simplified to single source-single sink systems. The rates of photosynthesis in the source leaves and the rates of translocation from the source leaves to the sink leaves were monitored, using a closed-loop, steady-state, $^{14}CO_2$-labelling system, as the temperature of the simplified plant was changed.

2. Literature Review

The translocation system of a plant is comprised of sources - regions which supply material to the system, sinks - regions which remove material from the system, and a network of connecting paths (Moorby, 1977). Although the mechanism of translocation has not been definitively determined, it is generally believed that movement from source to sink occurs by pressure-driven mass flow (Münch, 1930). This theory proposes that a high concentration of solutes in the source sieve tubes and a low concentration of solutes in the sink sieve tubes creates a turgor pressure gradient causing a bulk flow of solution from source to sink.

In an attempt to quantitate source-sink relationships Warren Wilson (1972) proposed the terms source strength and sink strength. Source strength was defined as

source strength = source size x source activity.

For a photosynthetic source this was interpreted as

assimilation rate = area x assimilation rate/area.

That is, source strength was defined as the total amount of carbon available for all leaf functions. However, not all of this carbon is available for translocation. Therefore, source strength is probably better expressed as export rate (Borchers-Zampini *et al.*, 1980). Similiarly, sink strength was defined as

sink strength = sink size x sink activity.

This was interpreted as

absolute growth rate = dry wt. x relative growth rate. That is, sink strength was defined as the rate of increase in dry weight. However, this only takes into account a portion of the carbon translocated to the sink. An accurate measure of sink strength should also include respirational losses (Wareing and Patrick, 1975).

2.1 Factors Affecting the Rate of Translocation

Much work has been done on determining the factors which control or influence the rate of translocation from source to sink (cf. Wardlaw, 1968; 1980; Gifford and Evans, 1981; Moorby, 1977). In general, factors in the source and the sink are more important in determining the rate of translocation than are factors in the path.

2.1.1 Source Factors

The source can influence the rate of export. The rate of export will be affected by the availability of translocate and the rate at which the available translocate is transferred to the conducting elements of the source (Geiger, 1979). The availability of translocate will be determined primarily by the rate of photosynthesis and the level of carbon reserves. Not all of the carbon assimilated by a source leaf is available for immediate export. Some is partitioned into starch. The fact that starch accumulation rates are inversely related to the length of the daily photosynthetic period indicates that the partitioning of

photosynthate into starch is a closely regulated process and not simply the result of a limitation on translocation (Chatterton and Silvius, 1979; 1980; 1981).

Under conditions of high sink demand, an increase in photosynthesis causes a proportional increase in translocation (Servaites and Geiger, 1974; Ho, 1976a; 1976b; 1978). As this relationship is independent of light or CO_2 concentration, Servaites and Geiger (1974) postulated that translocation is limited by sucrose synthesis. Ho (1976a; 1976b; 1978) has shown that there is a highly significant positive correlation between sucrose concentration and export in source leaves of tomato. However, this correlation is not always found (e.g. Sicher *et al.*, 1982). This is probably due to the partitioning of sucrose between mobile and non-mobile pools within the source leaf (Fisher and Outlaw, 1979). Ho (1976b) has demonstrated that export is determined by the concentration of mobile sucrose, and that the correlation between export and total sucrose concentration occurs when the mobile sucrose pool is in equilibrium with the total sucrose pool and a constant proportion of it.

This proportional relationship between photosynthesis and export holds only under conditions of high sink demand. Under conditions of low sink demand, the export rate is determined by the mobilizing ability of the sink, and excess carbon accumulates in the source (Ho, 1979).

The availability of translocate, and therefore the rate of export, will also be affected by the level of reserves. It has been shown that leaves with a greater concentration of reserves export carbon at a higher rate for a given photosynthetic rate (Ho, 1977), that when the rate of photosynthesis is very low the rate of translocation is maintained at a basal level by the breakdown of reserve material (Ho, 1976a), and that night transport is related to the content of reserves, rather than to the rate of photosynthesis in the previous light period (Ho, 1978).

The rate at which the available translocate is transferred to the conducting elements of the source will be determined by the availibility of energy in the source. Assimilates are produced in the source leaf mesophyll cells. Transfer to the sieve tubes involves, at least in some cases, transfer to the apoplast (Geiger *et al.*, 1974). This efflux is stimulated by K+ ions and may involve an active cotransport mechanism (Doman and Geiger, 1979). The assimilate, generally sucrose, is loaded from the apoplast into the sieve element-companion cell complex. Evidence indicates that sucrose is cotransported with protons down a proton gradient maintained by a proton-translocating ATPase located in the plasmalemma (Giaquinta, 1977; Malek and Baker, 1977). As the process by which assimilate is transferred to the conducting elements is energy dependent, any treatment which would affect source metabolism would affect the rate of export.

2.1.2 Sink Factors

The sink can influence import to the sink, export from the source, and source photosynthesis.

2.1.2.1 Import to the Sink

Translocation to a sink will be affected by the rate at which the sink removes translocate from the sieve tubes. The removal of translocate from the sieve tubes is dependent, directly or indirectly, on a supply of metabolic energy. It has been shown that conditions that inhibit the metabolism of the sink almost invariably decrease translocation to the sink (Geiger and Sovonick, 1975).

The cellular events associated with the removal of translocate from the sieve cells have received little attention and are only poorly understood. The work that has been done indicates that the cellular events, and the site or sites of energy dependence, vary with the specific sink (Giaquinta, 1980; Geiger and Fondy, 1980; Ho and Baker, 1982).

In growth sinks, transport from the sieve tubes to the surrounding parenchyma is thought to be symplastic. Exit from the sieve tubes would occur in direct response to the concentration gradient created by the depletion of the translocate by metabolic transformation in the parenchyma cells.

In storage sinks, assimilate is believed to enter the apoplast before being accumulated by the surrounding parenchyma. In some cases the removal of the translocate

from the sieve tubes is dependent on its utilization in the parenchyma cells. For example, in tomato, sucrose translocated to the fruit is converted to hexoses. As the fruit matures, its sucrose concentration increases and the import rate decreases proportionally. Evidence suggests that the rate of import is controlled by sink invertase activity (Walker and Ho, 1977a; Walker and Thornley, 1977; Walker et al., 1978)

In other cases, the removal of translocate from the sieve tubes is dependent on its compartmentation in the sink. Sugar beet roots and sugarcane stalks both accumulate sucrose. In sugar beet roots, sucrose enters the apoplast and is actively taken up into vacuoles of parenchyma cells (Wyse, 1979), possibly by a K^+ influx/proton efflux mechanism (Saftner and Wyse, 1980). In sugarcane stalks, sucrose enters the apoplast where it is hydrolysed to hexoses. The hexoses are then actively taken up by the parenchyma cells and reconverted to sucrose (Gaylor and Glasziou, 1972).

2.1.2.2 Export from the Source

An increase in import can result from an increase in export from the source, or from a redistribution of translocate away from less competitive sinks. Under conditions of low sink demand, export is less than maximum, and an increase in import can result from an increase in export. This is the case with girdled plants of *Phaseolus vulgaris* (Fondy and Geiger, 1980; Borchers-Zampini *et al.*,

1980). Under conditions of high sink demand, export rate is at a maximum. As starch reserves are not normally mobilized (Fondy and Geiger, 1980), except under conditions of low illumination (Ho, 1979; Fondy and Geiger, 1982), any increase in export must come from a redistribution of translocate away from less competitive sinks. This is the case with ungirdled plants of *P. vulgaris* and *Beta vulgaris*. Increasing sink demand resulted in an increase in import to the sink, but no increase in export from the source. The increase was the result of a redistribution of translocate away from the roots (Fondy and Geiger, 1980).

2.1.2.3 Source Photosynthesis

Many studies have demonstrated a positive correlation between sink demand and photosynthesis (Geiger, 1976). This indicates that there is some mechanism whereby source supply is regulated to meet sink demand. However, the nature of this mechanism is disputed. Some investigators feel that the accumulation of assimilates in the source leaf will inhibit photosynthesis. Specifically, it has been suggested that the accumulation of assimilates may inhibit photosynthesis via endproduct inhibition, distortion of chloroplasts, impedance of intracellular CO_2 diffusion, shading of chloroplasts, or hormone production. Other investigators feel that when inhibition does occur it is not caused by assimilate accumulation but rather by nutritional or long distance hormonal factors.

The difficulty in discerning the mechanism of regulation lies in demonstrating that assimilate accumulation and inhibition of photosynthesis are causally related and not just correlated. Studies of intact plants have often shown that as a plant goes through developmental or diurnal changes, photosynthesis is negatively correlated with starch level. Geiger (1976) points out that this merely illustrates the high degree of integration that is to be expected in a successful, complex system and does not indicate causation. Studies in which the source:sink ratio has been altered by excising or shading plant parts or otherwise manipulating the plant, have also often shown that photosynthesis is negatively correlated with starch level. Neales and Incoll (1968) point out that these treatments could induce hormonal or nutritional imbalances, as well as changes in starch level, so again causation cannot be proven.

Although many studies have shown a negative correlation between photosynthesis and starch accumulation, many others have failed to show such a correlation. These contradictory results indicate that the situation is complex. Some authors (e.g., Geiger, 1976) claim that this very complexity argues against a simple negative feedback system. However, these contradictory results may simply indicate that a negative feedback system operates only under certain specified conditions. Usually the data on feedback inhibition are analyzed irrespective of the method used to increase or

decrease the source:sink ratio or the plant material used. A close examination of the literature reveals that these may be important factors. The regulation of source supply to meet sink demand appears to involve at least three different phenomena:

1. When assimilate levels in source leaves are raised to very high levels, photosynthesis is often inhibited. Exposing source leaves of soybeans to high levels of CO_2 for 12.5 hours (Nafziger and Koller, 1976), exposing *Beta vulgaris* to 48 hours of continuous light (Milford and Pearman, 1975), and exposing cotton to high levels of CO_2 for 10 days (Mauney *et al.*, 1979) all resulted in increased levels of starch and decreased photosynthesis.

There is some indication that this inhibition may be due to starch accumulation impeding intracellular CO_2 transport. Nafziger and Koller (1976) found that the decrease in photosynthesis that was associated with starch accumulation resulted from an increase in mesophyll resistance. Also, Mauney *et al.* (1979) found that the inhibition of photosynthesis that was associated with starch accumulation in cotton was only evident when photosynthesis was measured under low CO_2; it was not evident when measured under high CO_2 levels.

Very high levels of starch are required for inhibition of photosynthesis to occur. Nafziger and Koller (1976) found that, in soybean, photosynthesis was significantly inhibited only at starch levels greater that 2.0 mg cm^{-2}. This may

explain some of the negative results of other investigators. Crookston (1974) did not find a negative correlation between starch accumulation and photosynthesis in *Phaseolus vulgaris*, but the maximum starch level obtained was only 0.2 mg cm^{-2}. Mauney *et al.* (1979) did not find a negative correlation between starch accumulation and photosynthesis in soybean, sunflower, or sorghum. The maximum starch levels obtained in all these species were lower than the maximum starch level obtained in cotton, which did show a negative correlation.

However, low maximum starch levels do not explain all negative results. Potter and Breen (1980) exposed sunflower and soybean to 52 hours of continuous light and found that even though there was a large accumulation of starch, photosynthesis was only slightly inhibited.

2. When assimilate levels in the source leaf are depleted to very low levels, photosynthesis can increase. Thorne and Koller (1974) decreased source:sink ratio by shading all except one source leaf of *Glycine max*. Starch levels decreased to less than 2% of dry weight and photosynthesis increased curvilinearly over 8 days. This increase was a complex phenomenon involving increases in P_i concentration and RuBP carboxylase activity. The authors concluded that the increase in photosynthesis was the result of hormonal changes, and was not the result of a decrease in starch level. However, there remains the possibility that the decrease in starch level could have triggered the change

in hormonal activity.

3. Reducing or eliminating sink demand can cause a decrease in photosynthesis. Setter *et al.* (1980a & b), working with *Glycine max*, found that both pod removal and petiole girdling resulted in a rapid decrease in photosynthesis. This decrease, which was correlated with a decrease in stomatal resistance and an increase in ABA level, was independent of starch accumulation. The authors concluded that the increase in ABA and concomitant stomatal closure and decrease in photosynthesis was the result of decreased ABA translocation out of the leaf. In contrast, Geiger (1976), working with *Phaseolus vulgaris*, found that neither petiole girdling nor sink removal caused a decrease in photosynthesis over 30 hours. It may be important that Geiger used young plants, whereas Setter *et al.* used mature plants at a reproductive stage of developement.

2.1.3 Path Factors

The path does not appear to exert any influence over the rate of translocation, at least under non-stress conditions. Passioura and Ashford (1974) demonstrated that when wheat seedlings were forced to grow with only one seminal root, rates of mass transfer many times higher than any previously reported occurred in the phloem of the root base. Also, it has been demonstrated that severing one half of the vascular tissue in the peduncle of wheat (Wardlaw and Moncur, 1976) or the culm of sorghum (Muchow and Wilson,

1976) has no effect on yield. These experiments show that the transport path appears to be more than adaquate to meet the demands made on it.

2.2 Temperature Effects on Translocation

Many studies have been done on the effect of temperature on translocation. Most of these involved varying the temperature of a specific plant part. In general, they have demonstrated that, while both source and sink temperature greatly affect translocation, path temperature has little effect, except at temperature extremes.

2.2.1 Source Temperature

The rate of translocation from a source is dependent on source metabolism, therefore it will be affected by source temperature. Temperature will affect both the availability of translocate, and the rate at which the available translocate is transferred to the sieve tubes.

Photosynthesis is strongly affected by temperature. The optimum temperature for photosynthesis varies widely between species, and there is a marked tendency for the optimum for any given plant to reflect its growth temperature. Also, the effect of temperature on photosynthesis is influenced by other environmental factors, especially light intensity and intercellular CO_2 concentration (Berry and Björkman, 1980).

Experiments to determine the effect of temperature on export must be carefully designed so that the effect of

temperature on export can be separated from its effect on photosynthesis. The effect of temperature on export has been demonstrated using non-photosynthetic sources. Lateral movement of solutes into the sieve tubes of willow (Ford and Peel, 1966), and sugar secretion by cells surrounding the sieve tubes in *Yucca* (Tammes *et al.*, 1969) were both inhibited by low temperature. The effect of temperature on export has also been demonstrated by comparing the rate of photosynthesis with the rate of export. Wardlaw (1974), working with wheat, demonstrated that while flag leaf photosynthesis was optimal at 15°C, vein loading, defined as the loss of ^{14}C from the leaf, continued to increase to 30°C.

2.2.2 Sink Temperature

The rate of translocation to a sink is dependent on sink metabolism and therefore will be affected by sink temperature. A number of studies have demonstrated the effect of sink temperature on translocation. Increasing sink temperature increased translocation to the fruits of *Pisum sativum* (Williams and Marinos, 1978), *Glycine max* (Thorne, 1982), and tomato (Walker and Ho, 1976; 1977b). Movement of assimilate to the ear of wheat was optimal at an ear temperature of 30°C (Wardlaw, 1974). Chilling the sink region of *Beta vulgaris* caused an inhibition of translocation (Geiger, 1966). In sugar cane, a root temperature of 17°C inhibited translocation to the roots

(Hartt, 1965). Movement of assimilate into tissue surrounding the path was reduced by low temperature in *Lolium temulentum* (Wardlaw, 1972).

The increased translocation to the sinks in response to increased temperature was undoubtedly due to the increased metabolism in the sink. For example, in tomato, where the import rate has been shown to be inversely proportional to the sucrose concentration in the fruit, low temperatures increase the sucrose concentration of the fruit, probably by inhibiting invertase activity (Walker and Thornley, 1977; Walker *et al.*, 1978). However, there is evidence of another effect. Williams and Williams (1978) demonstrated that not only was heating just the basipetal or acropetal half of a pod of *Pisum* as effective as heating the whole pod in increasing the incorporation of ^{14}C assimilate in the ovules, but also that there was a decreased amount of ^{14}C assimilate remaining in the leaf with increased temperature of the pod, even with the ovules removed. From these results the authors speculated that export from the source may have been affected by a stimulus emanating from ovarian tissue.

2.2.3 Path Temperature

Studies in which path temperature was varied indicate that while the effect of temperature on translocation is minimal over a moderate range, inhibition does occur at temperature extremes (Swanson and Böhning, 1951; Webb and Gorham, 1965). The temperatures at which inhibition occurs

vary with the species studied (Webb, 1967; Wardlaw, 1974).

2.2.3.1 Low Temperature Inhibition

Lowering the temperature of a portion of the path below a critical temperature results in increased impairment of translocation. Above this critical temperature translocation has a Q_{10} of 1.0 to 1.5; below, it has a Q_{10} greater than 4 (Giaquinta and Geiger, 1973; Lang, 1974). Plants can be grouped into two categories based on the critical temperature at which this increased impairment occurs. Chilling-sensitive plants have a critical temperature of approximately 10°C; chilling-insensitive plants have a critical temperature of approximately -0.5°C (Geiger, 1969; Giaquinta and Geiger, 1973).

Chilling-Sensitive Plants

Chilling a portion of the path of a chilling-sensitive plant below approximately 10°C results in a drastic prolonged inhibition of translocation. This is known to occur in bean (Child and Bellamy, 1919; Curtis, 1929; Curtis and Herty, 1936; Swanson and Böhning, 1951; Swanson and Geiger, 1967; Geiger and Sovonick, 1970; Giaquinta and Geiger, 1973; Minchin *et al.*, 1983), broad bean (Faucher *et al.*, 1982), soybean (Vernon and Aronoff, 1952; Thrower, 1965), squash (Webb and Gorham, 1965; Webb, 1967; Webb, 1971), *Sorghum* (Wardlaw and Bagnell, 1981), rib grass (Faucher *et al.*, 1982), a southern ecotype of Canadian thistle (Bayer, in Geiger, 1969), and two gymnosperm species

(Watson, 1980). Recovery at the chilling temperature either does not occur or occurs very slowly over many hours or days (Swanson and Böhning, 1951; Geiger and Sovonick, 1970; Geiger, 1969; Webb, 1971; Giaquinta and Geiger, 1973). Translocation does resume on rewarming the cooled region, after a short lag (Thrower, 1965; Geiger and Sovonick, 1970; Webb, 1971 Minchin *et al.*, 1983).

Chilling-Insensitive Plants

Chilling part of the path of a chilling-insensitive plant such as *Lolium* (Wardlaw, 1972), wheat (Wardlaw, 1974; Faucher *et al.*, 1982), willow (Watson, 1975), *Nymphoides* (Lang, 1974), *Yucca* (Tammes *et al.*, 1969), sugar beet (Swanson and Geiger, 1967; Geiger and Sovonick, 1970; Giaquinta and Geiger, 1973), maize (Faucher *et al.*, 1982), or a northern ecotype of Canadian thistle (Bayer, in Geiger, 1969) as low as 0°C results in little or no inhibition of translocation. The speed of translocation is also maintained in the cooled paths (Wardlaw, 1972; 1974; Watson, 1975; Geiger and Sovonick, 1970).

Time course studies with sugar beet (Swanson and Geiger, 1967; Geiger and Sovonick, 1970; Giaquinta and Geiger, 1973), *Nymphoides* (Lang,1974), *Ipomea* (Minchin and Thorpe, 1983) and a northern ecotype of Canadian thistle (Bayer, in Geiger, 1969) have demonstrated that chilling can cause a severe transitory inhibition of translocation. Recovery, to either a rate similar to the prechilling rate (e.g., sugar beet) or to a rate just slightly less than the

prechilling rate (e.g., *Nymphoides*) occurs within 2 to 5 hours. This inhibition is associated with a decrease in speed, and recovery is due to a restoration of speed (Geiger and Sovonick, 1970). Minchin and Thorpe (1983) have shown that this 'cold shock' effect requires a very rapid rate of cooling. However, their minimum temperature was only 10°C. It is possible that with a very low chilling temperature the rate of cooling may not be as important a factor.

Mechanism of Chilling Inhibition

Below the critical temperature translocation has a Q_{10} greater than 4. This is consistent with a severe disruption of the translocation system. Giaquinta and Geiger (1973) demonstrated that the sieve pores of chilling sensitive plants chilled to 0°C were occluded by cytoplasmic material and they suggested that this occulsion was the cause of the inhibiton. They further suggested that the physical damage was caused by a transition of membrane lipids from a liquid to a coagel. In chilling-sensitive plants, whose membrane lipids have a greater degree of fatty acid saturation, this phase change occurs at approximately 10°C; in chilling-insensitive plants it occurs at approximately 0°C.

Above the critical temperature, translocation has a Q_{10} of 1.0 to 1.5. Lang (1978) has suggested that this long-term, slight temperature dependence is caused by changes in the viscosity of the phloem sap, which theoretically should have a Q_{10} of 1.3. Why some plants should exhibit this long-term dependence and other plants

not, is not known. The short-term inhibition of translocation that results from rapid cooling may result from structural changes (Geiger, 1969; Geiger and Sovonick, 1970; Ferrier and Christy, 1975). Recovery may be due to a pressure increase sufficient to overcome an increased resistance along the pathway or it could be due to a reversal of any processes which led to increased resistance (Geiger and Sovonick, 1970).

Faucher *et al.* (1983) have recently suggested that it is the absence of P-protein which confers chilling insensitivity. They showed that maize and wheat, which do not have P-protein, are not chilling sensitive, while broad bean and rib grass, which do have P-protein, are chilling sensitive. However, sugar beet, a classic-chilling insensitive plant, does have P-protein (Esau *et al.*, 1967). Therefore, their hypothesis is not valid.

2.2.3.2 High Temperature Inhibiton

Warming a portion of the path above 40 to 50°C also leads to inhibition (Swanson and Böhning, 1951; Webb and Gorham, 1965; Webb, 1967; Wardlaw, 1974). In contrast to low temperature inhibition, high temperature inhibition generally increases with time (Swanson and Böhning, 1951; Wardlaw, 1974). The mechanism of high temperature inhibition, which is not well understood, appears to be complex, involving a number of phenonema. McNairn and Currier (1968) demonstrated that the inhibition of translocation that resulted when a 4 cm portion of a cotton

hypocotyl was heated to 40°C for 15 min was the result of the constriction of the sieve pores by callose depostion. This inhibition was reversible, with translocation returning to normal within 6 hours. However, the effects of high temperature are often irreversible (Webb and Gorham, 1965). In these cases, the inhibition may be due to the denaturation and coagulation of the sieve tube contents (Webb, 1967).

2.2.4 Whole Plant Temperature

While much work has been done on the effects of varying the temperature of individual plant parts, only a few studies have been done on the effects of varying the temperature of the whole plant. Curtis and Herty (1936) examined the effect of whole plant temperature on translocation in bean. Estimating translocation from the loss of dry matter in leaves of plants held in darkness, they found that an ambient temperature of 1 or 4.5°C significantly reduced translocation, compared to an ambient temperature of 25°C. Hewitt and Curtis (1948), using similar techniques, measured the effect of temperature on translocation in bean, milkweed, and tomato. In all three species, translocation was optimal at approximately 25°C. In contrast, respiration continued to increase to 40°C. It is probable that the low optimum for translocation was due to the depletion of carbohydrate reserves by respiration at the higher temperatures.

Whittle (1964), estimating translocation from radioactivity profiles, found that translocation in *Pteridium* showed a Q_{10} of 2.9 over the temperature range 13-30°C. However, this experiment failed to separate the effect of temperature on translocation from its effect on photosynthesis. McNairn (1972) examined translocation in field grown cotton and found that at high field temperatures translocation was inhibited both by callose deposition and by some other undetermined factor.

3. Materials and Methods

3.1 Plant Material

Phaseolus vulgaris L. cv. Black Valentine seeds (Rogers Co., Idaho Falls, Idaho) were imbibed for 3 days in aerated saturated $CaSO_4$ solution. The imbibed seeds were placed on sloping enamel trays, between paper towelling moistened with the $CaSO_4$ solution, and incubated, at room temperature, in the dark, for approximately 6 days. The etiolated seedlings were transferred to 2-litre opaque plastic pots containing full strength Hoagland's solution with Fe as FeEDTA (Hewitt, 1966). Initially, ten seedlings were placed in each pot; subsequently, selected seedlings were transferred to similar individual pots.

The pots were placed in a controlled enviroment chamber (Enviromental Growth Chambers, Chagrin Falls, Ohio). The Hoagland's solution was continually aerated. Air temperature was maintained at 20°C, relative humidity at 55%. The plants were exposed to a 14-hour photoperiod. A light intensity of 300 $\mu E\ m^{-2}s^{-1}$ was supplied by a mixture of fluorescent tubes and incandescent bulbs for 12 hours. This was preceded and followed by 1 hour of a light intensity of 25 $\mu E\ m^{-2}s^{-1}$ supplied by the incandescent bulbs alone.

3.2 Simplified Source-Sink System

The plants were grown to the stage where the terminal leaflet of the first and only visible trifoliate leaf was approximately 3-4 cm in length. The day before an experiment, one primary leaf, the two lateral leaflets of the first trifoliate leaf, the apex and all buds were removed. The stem was heat girdled below the cotyledonary node with a curved soldering iron tip to prevent the roots acting as sinks. This resulted in a single source-single sink system, the single source being the remaining primary leaf, the single sink being the central leaflet of the first trifoliate leaf (Fig. 1).

3.3 Measurement of Net Photosynthesis and Translocation

The rate of net photosynthesis in the source leaf and the rate of translocation from the source leaf to the sink leaf were determined using a closed-loop, steady-state, $^{14}CO_2$-labelling system (Fig. 2). The system was designed by Hoddinott et al.(1979) and is similar in principle to an original design of Geiger and Swanson (1965).

The source leaf was placed inside the cuvette which, when sealed, formed part of the closed loop. The sink leaf was mounted on a Geiger-Müller tube which was connected to a ratemeter-recorder assembly. The gas in the loop was constantly circulated by an air pump, the flow rate was monitored, and a helical manometer ensured that the loop operated at atmospheric pressure. The air was dehumidified

Figure 1. *Phaseolus vulgaris* simplified to a single source-single sink system. The horizontal bar represents the place the stem was heat girdled. The round dot represents the cotyledonary node.

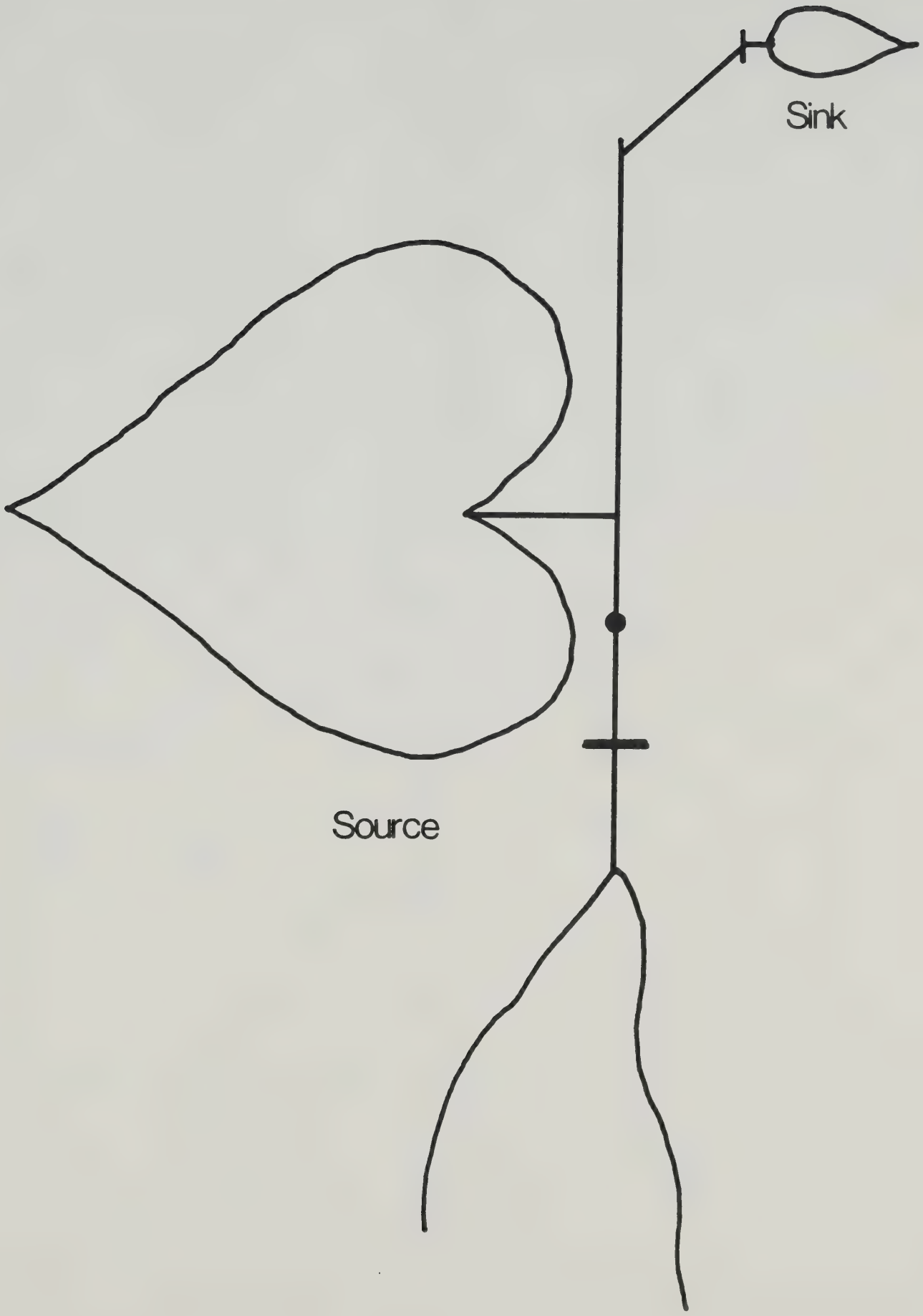
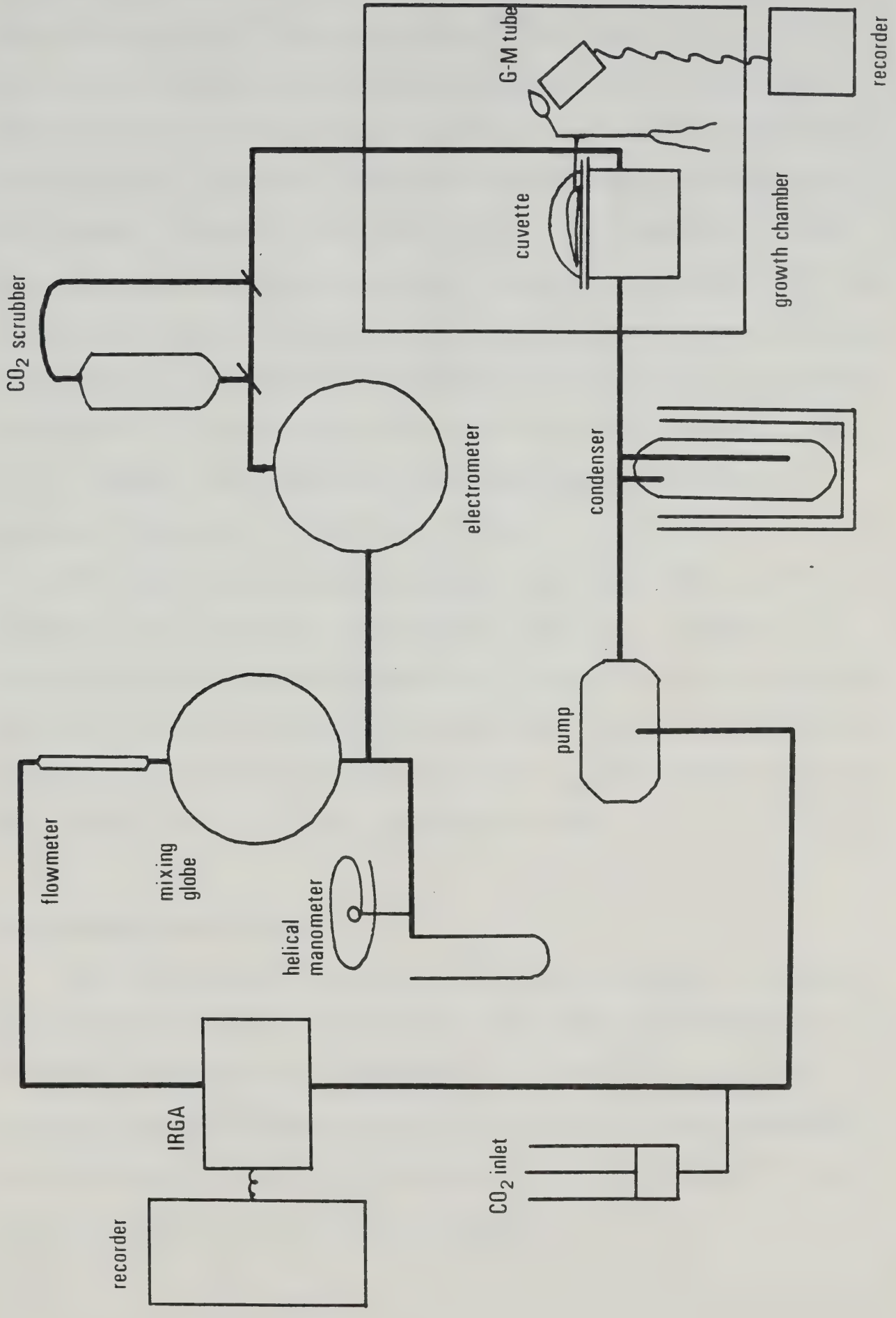

Sink
Source

Figure 2. Schematic diagram of the closed-loop, steady-state, $^{14}CO_2$-labelling system.


recorder
G-M tube
cuvette
growth chamber
CO_2 scrubber
electrometer
condenser
pump
flowmeter
mixing globe
helical manometer
IRGA
CO_2 inlet
recorder

by a water condenser. An Infrared Gas Analyzer (IRGA) monitored the CO_2 concentration in the loop, and an ionization chamber-electrometer assembly monitored the specific activity of $^{14}CO_2$. The CO_2 level was maintained at 308±5 ppm by a negative feedback system. When the CO_2 level fell below 308 ppm a motor driven syringe pump was turned on, introducing CO_2 of a constant specific activity into the loop; when the CO_2 concentration rose above 308 ppm the pump was turned off. The mixing globe ensured that the gas being introduced was throughly mixed with the gas already in the loop. Excess $^{14}CO_2$ could be removed from the system by opening the loop to the CO_2 scrubber.

The rate of net photosynthesis was calculated from the volume of CO_2 required to keep the loop at a constant CO_2 concentration; this was determined from the running time and delivery rate of the syringe pump. The rate of translocation was calculated from the slope of the recorder trace showing the accumulation of ^{14}C in the sink leaf.

3.4 Temperature Control

The cuvette was located in a growth chamber, allowing various enviromental variables, including temperature, to be altered. Changing the temperature of the plant involved changing the air temperature of the chamber, the temperature of the Hoagland's solution the roots were immersed in, and the air temperature inside the cuvette.

The air temperature of the chamber was altered with the chamber controls. The temperature of the roots was altered by slowly exchanging the initial Hoagland's solution with solution of the appropriate temperature. The air temperature inside the cuvette was controlled by mounting the cuvette on a Peltier cold plate through which a glycol solution was circulated by a circulating refrigerating glycol bath. The cold plate was controlled by a comparison circuit and would cool whenever the temperature inside the cuvette was higher than the temperature outside the cuvette (cf. van Zinderen Bakker, 1974). When a drop to a low temperature was required, the gylcol solution was also circulated through 1/4in diameter Tygon tubing wrapped around the base of the cuvette.

Initial attempts to achieve a reasonably rapid temperature drop inside the cuvette when the chamber air temperature was dropped involved pretreating the air entering the cuvette by passing it through 12 feet of coiled copper tubing immersed in a cold glycol solution. This treatment had no appreciable effect.

The temperatures of the air inside the cuvette, the air outside the cuvette, the source leaf, the stem, the sink leaf, and the root solution were monitored using copper-constantan thermocouples connected to a digital thermometer. All plant parts could be held within 0.5°C of the desired temperature. All changes in temperature could be completed within 30 min.

3.5 Experimental Design

The day before an experiment, the source leaf of a plant, simplified to a single source-single sink system, was placed in the cuvette. The plant was allowed to equilibrate overnight, at 20°C, with air flowing through the cuvette. In the morning, the cuvette was introduced into the closed loop. After approximately 90 min the plant reached isotopic equilibrium, and control rates of net photosynthesis and translocation were determined. The temperature of the plant was then altered to an experimental value between 5 and 35°C, and after equilibrium had again been established, rates of net photosynthesis and translocation at the experimental temperature were determined. The rates obtained at the experimental temperature were converted to relative values by arbitrarily setting the rates at 20°C to 1.00. A relative translocation:photosynthesis (T:P) ratio was also calculated. During the experiment, the source leaf was exposed to a light intensity of 150 μE $m^{-2}s^{-1}$, supplied by fluorescent tubes. The light intensity had to be low because the volume of CO_2 available for any one experiment was limited to 50 cc by the capacity of the syringe pump. At the end of an experiment, the source leaf was removed from the plant, dried to a constant weight in an oven, and its dry weight determined. Three to five plants were run at each experimental temperature.

4. Results

The values of photosynthesis and translocation obtained from different plants exposed to the same experimental temperature varied widely, even though the plants were grown under similar conditions. Therefore, the rates of photosynthesis and translocation obtained by individual plants at the experimental temperature were expressed relative to the rates obtained at 20°C.

The results of a typical experiment are illustrated in Fig. 3. Translocation rates, photosynthesis rates, and T:P ratio values at 20°C were arbitrarily set to 1.00. A decrease in temperature from 20 to 15° C resulted in a relative value of 1.12 for photosynthesis, 0.62 for translocation, and 0.55 for the T:P ratio. These relative values, unlike the absolute values, show a marked consistency (Table 1). The relative values calculated for individual plants were averaged and plotted on semilog graphs.

4.1 Net Photosynthesis

Maximum net photosynthesis occurred between 10 and 15°C (Fig. 4 and Table 2). Above 15°C, net photosynthesis was slightly inhibited; below 10°C, it was strongly inhibited. At 5°C, photosynthesis did not reach a steady value, but slowly decreased with time. Therefore, only the last photosynthetic determination, from 160 to 200 min after the temperature change, was used.

Figure 3. Changes in net photosynthetic rate and translocation rate that occurred when the temperature of a plant was changed from 20 to 15 C. P=net photosynthesis; T=translocation; T:P=translocation:photosynthesis ratio. The arrow indicates the time of the temperature change. Error bars represent 2 standard deviations.

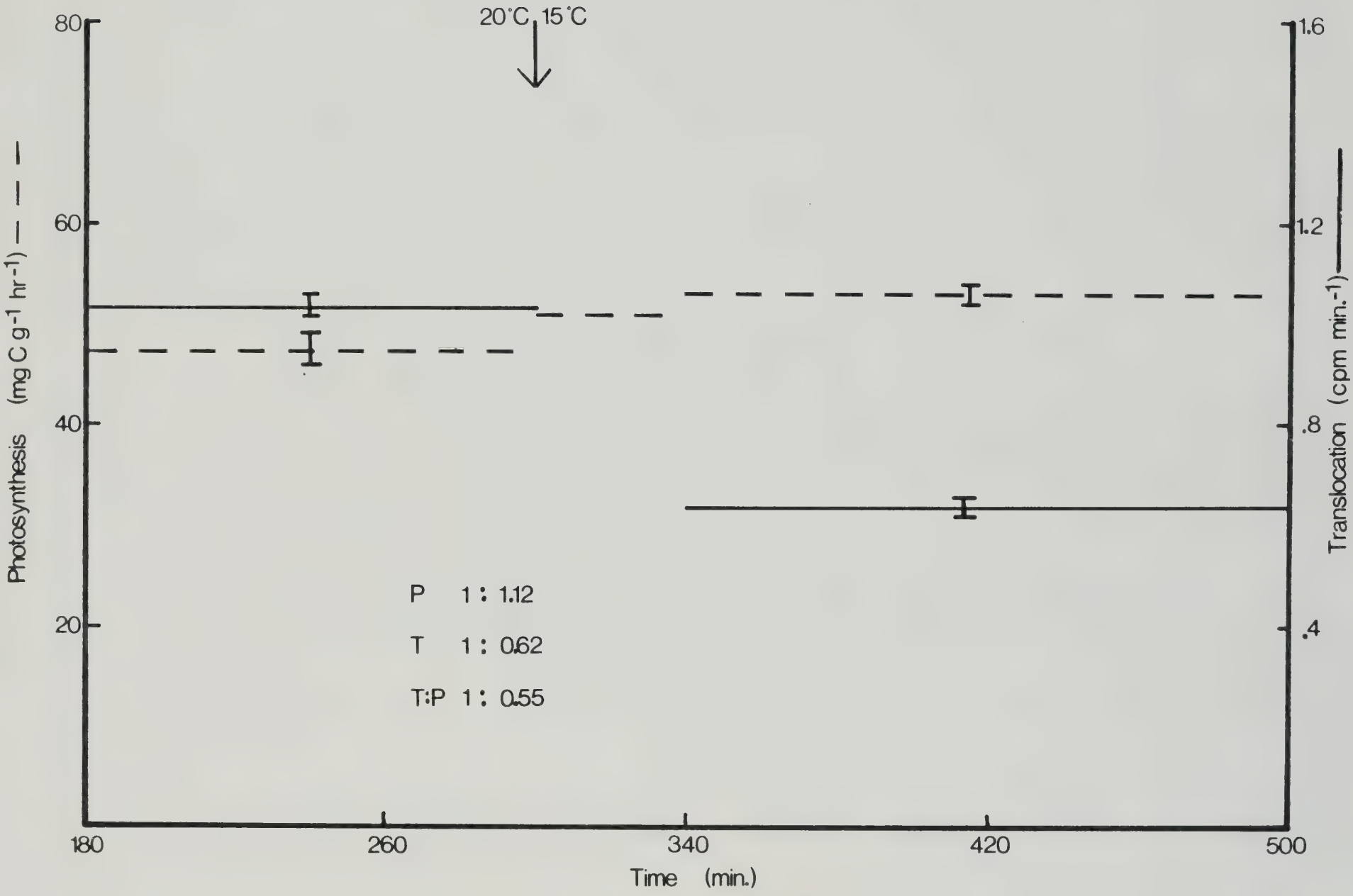

20°C, 15°C
80
60
40
20
1.6
1.2
.8
.4
Photosynthesis (mg C g-1 hr-1) — — —
Translocation (cpm min.-1) ——
P 1 : 1.12
T 1 : 0.62
T:P 1 : 0.55
180
260
340
420
500
Time (min.)

Table 1. Relative net photosynthetic rates, translocation rates, and translocation:photosynthesis ratios at different temperatures.

Temp (°C)	T	P	T:P
5	0.21	0.39	0.54
	0.24	0.40	0.60
	0.25	0.38	0.67
	0.25	0.36	0.69
10	0.32	1.03	0.31
	0.34	1.20	0.28
	0.31	1.03	0.30
	0.30	0.98	0.31
15	0.58	1.14	0.51
	0.69	1.28	0.54
	0.62	1.12	0.55
	0.69	1.09	0.63
	0.70	1.13	0.62
20	1.00	1.00	1.00
	1.00	1.00	1.00
	1.00	1.00	1.00
25	1.56	0.96	1.62
	1.69	0.99	1.71
	1.29	0.97	1.33
	1.37	0.96	1.43
30	1.38	0.91	1.51
	1.65	0.85	1.95
	1.82	0.88	2.07
	1.72	0.88	1.96
35	1.85	0.76	2.69
	1.71	0.83	2.42
	1.96	0.72	2.70

Figure 4. The effect of temperature on the relative net photosynthetic rate. Each point represents the mean of 3-5 plants. Error bars represent 95% confidence limits.

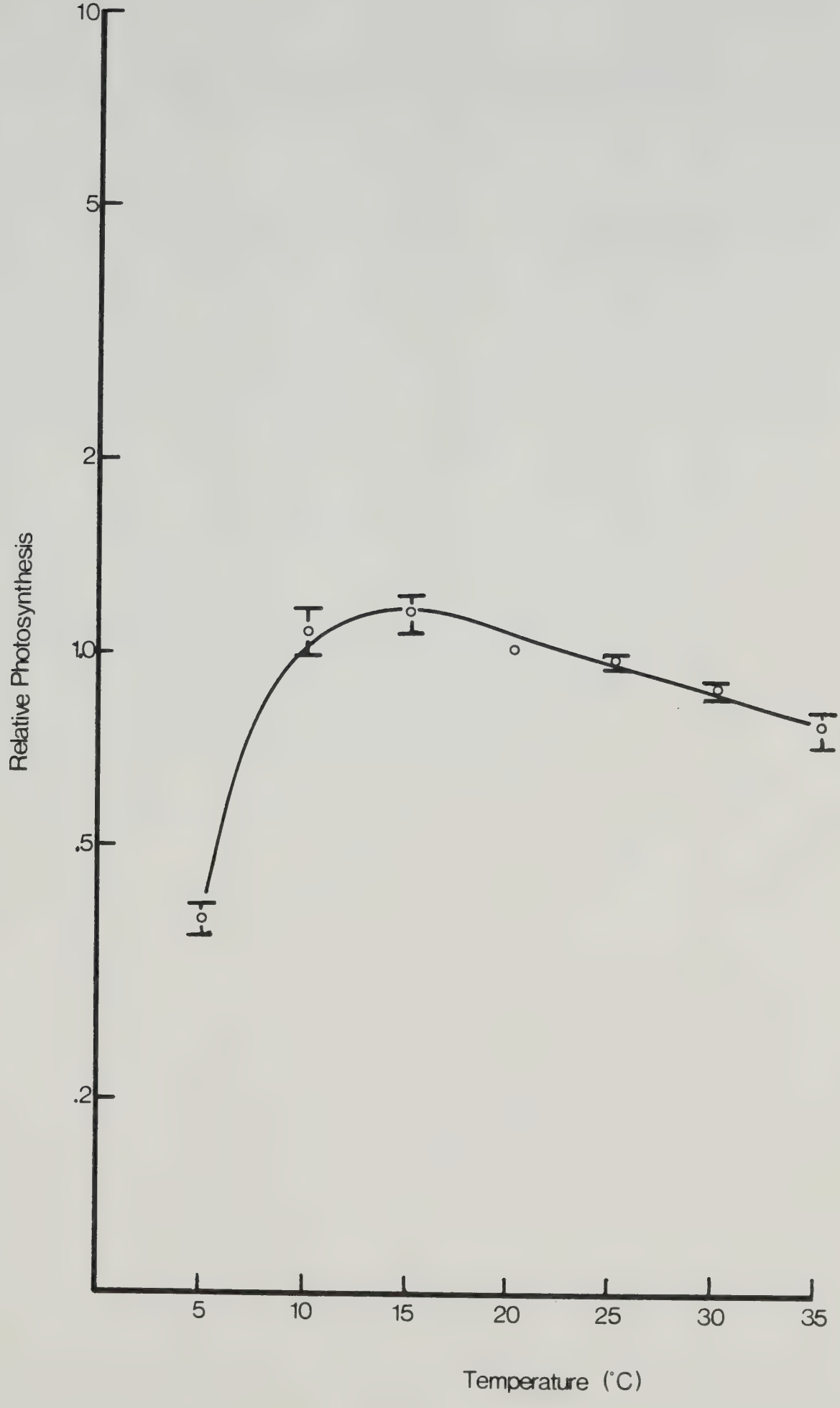

10
5
2
1.0
.5
.2
Relative Photosynthesis
5
10
15
20
25
30
35
Temperature (°C)

Table 2. Mean photosynthetic rates at different temperatures (plusminus 2 standard deviations).

Temperature (°C)	Net Photosynthesis (ug m^{-2} s^{-1})
5	23.4 ± 7.2
10	48.2 ± 6.6
15	59.2 ± 11.3
20	53.2 ± 3.9
25	49.4 ± 16.0
30	46.4 ± 6.0
35	45.1 ± 6.9

4.2 Translocation

The rate of accumulation of ^{14}C in the sink leaf increased as temperature increased from 5 to 35°C (Fig. 5). Above 25°C the rate of increase was markedly reduced, below 10°C the rate of decrease was slightly reduced. At 35°C there was a decrease in the rate of accumulation with time. Therefore, the rate of translocation at 35°C was estimated only from data points between 40 and 120 min after the temperature change, a period during which the translocation rate had stopped increasing from the temperature change and not yet begun to decline.

4.3 Translocation:Photosynthesis Ratio

The T:P ratio gives a measure of the proportion of the current photosynthate being translocated (Servaites and Geiger, 1974). The T:P ratio decreased as temperature decreased from 35 to 10°C (Fig. 6). A further decrease in temperature to 5°C caused an increase in the T:P ratio.

Figure 5. The effect of temperature on the relative translocation rate. Each point represents the mean of 3-5 plants. Error bars represent 95% confidence limits.

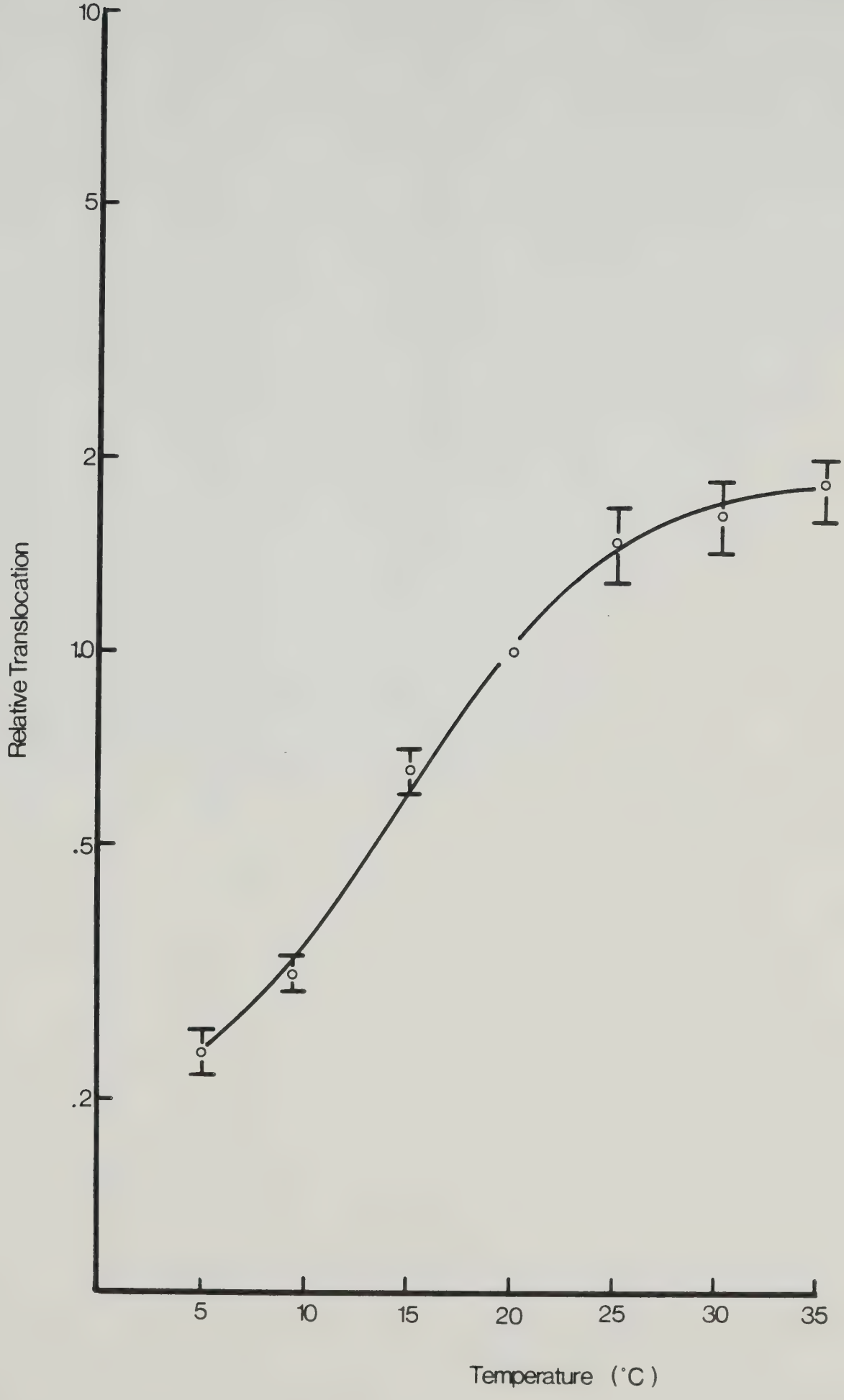
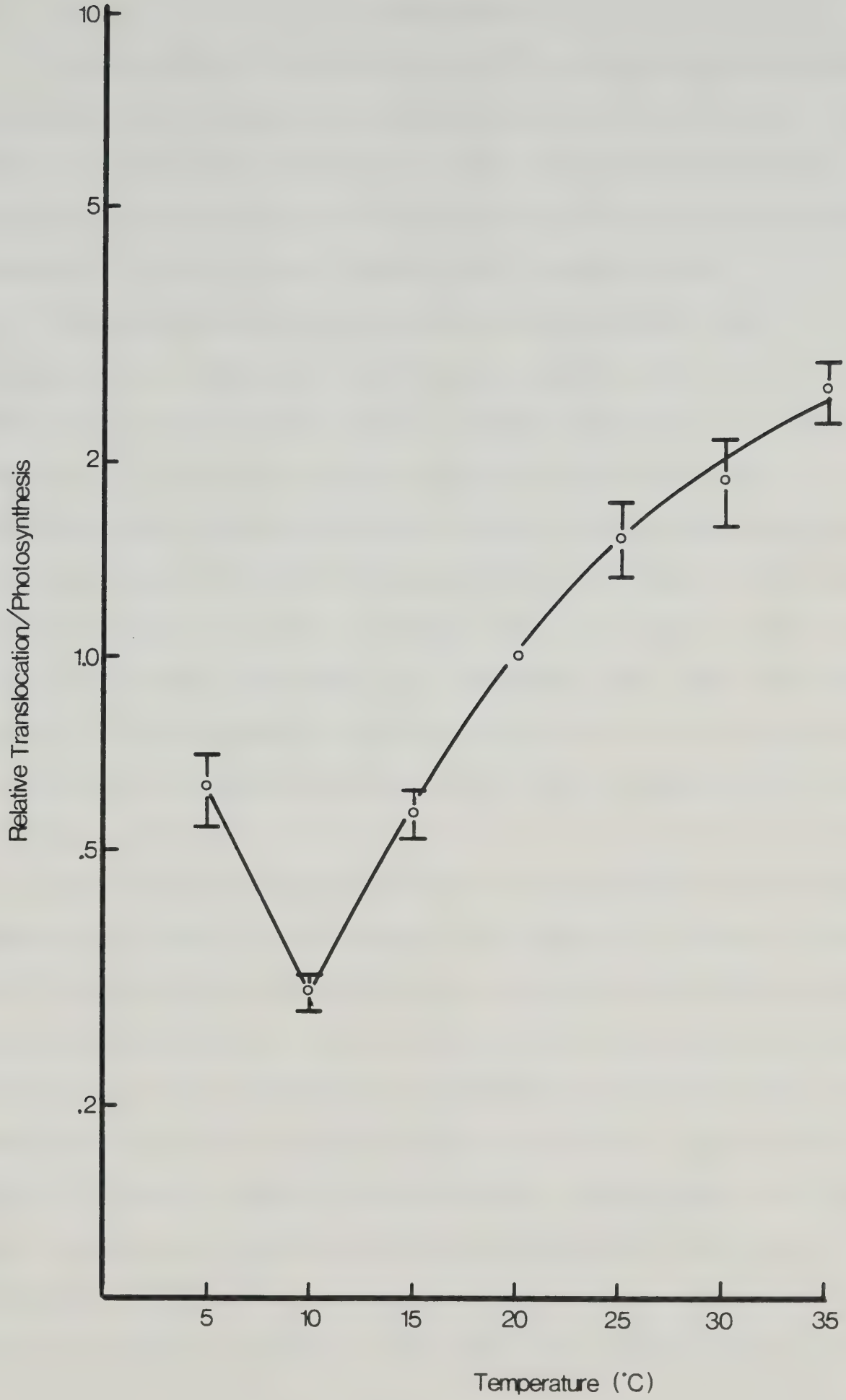

10
5
2
1.0
.5
.2
Relative Translocation
5
10
15
20
25
30
35
Temperature (°C)

Figure 6. The effect of temperature on the relative translocation:photosynthesis ratio. Each point represents the mean of 3-5 plants. Error bars represent 95% confidence limits.


10
5
2
1.0
.5
.2
Relative Translocation/Photosynthesis
5
10
15
20
25
30
35
Temperature (°C)

5. Discussion

The purpose of this study was to determine the effect of whole plant temperature on translocation. A single source-single sink system was used. This eliminated the possibility of changes in the partitioning of assimilates between different plant organs with temperature.

These experiments monitored photosynthesis and translocation using a closed-loop, steady-state, $^{14}CO_2$-labelling system. Such a system supplies the source leaf with $^{14}CO_2$ of a constant specific activity and concentration. When the plant reaches isotopic saturation, the label content of an intermediate pool, such as sucrose, becomes constant, and a terminal pool, such as a sink leaf, will accumulate the label at a constant rate. Any variation in the ^{14}C accumulation rate of the sink leaflet will be a measure of a corresponding change in the translocation rate (Geiger, 1980).

Both net photosynthesis and translocation varied with temperature. Net photosynthesis was optimal between 10 and 15°C. Although photosynthesis was greatly inhibited below this temperature, it was only slightly inhibited above this temperature. The temperature response of photosynthesis is dependent on other environmental conditions, especially light intensity and CO_2 concentration. When these are higher the temperature response is more pronounced (Berry and Bjorkman, 1980). The low temperature optimum and relative lack of response found in the study are probably due to the

low light intensity (150 $\mu E\ m^{-2}\ s^{-1}$) and the low CO_2 concentration (308 ppm) the source leaf was exposed to.

Translocation, as measured by the accumulation of ^{14}C in the sink leaf, also varied with temperature. However, the accumulation of ^{14}C represents only a portion of the total ^{14}C translocated to the sink. It will not include that ^{14}C respired and not refixed by sink leaf photosynthesis. This may be a significant factor, as the amount of respiration will vary with temperature.

As both photosynthesis and translocation were affected by temperature, it is necessary to determine whether part of the variation in translocation was due to the variation in the availability of translocate. An examination of the literature shows that photosynthesis only affects translocation under certain conditions. The necessity of maintaining a supply of carbohydrates for sinks during the daily dark period requires that a certain percentage of the current photosynthate be partitioned into starch. This has been shown to be a closely regulated process (Chatterton and Silvius, 1980). This requirement for starch deposition has priority over sink demand for assimilate (Fondy and Geiger, 1980). When the proportion of current photosynthate being exported is at a maximum, the rest being required for starch deposition and source leaf maintainance, an increase in photosynthesis will result in a proportional increase in translocation, and translocation will be a constant proportion of photosynthesis (Servaites and Geiger, 1974;

Ho, 1976) However, when the proportion of current photosynthate being exported is not at a maximum, an increase in photosynthesis will not cause an increase in translocation, at least not in the short term. The amount of carbon translocated will depend on the requirement of the sink, and excess carbohydrate will accumulate in the source leaf (Ho, 1979).

In the present situation, if it is assumed that the proportion of photosynthate required for storage does not change with temperature, then there is a criterion for establishing whether the change in the accumulation rate of the sink leaf is a result of a change in photosynthesis. If the T:P ratio is a constant maximum, this implies that any change in the accumulation rate would be due to a change in photosynthesis. Alternatively, if the T:P ratio is not a constant maximum, then this implies that the accumulation rate is limited by translocation.

The T:P ratio is maximum at 35°C, decreases as temperature is decreased to 10°C, and then slightly increases as temperature is further decreased to 5°C. This illustrates that less than the maximum proportion of photosynthate was being translocated, at least through the temperature range 5 to 30°C, and, in the absence of data at a higher temperature, possibly at 35°C as well. This implies that the variation in the rate of ^{14}C accumulation was the result of an effect of temperature on translocation, and not due to an effect on the availability of translocate.

The results illustrate a pronounced effect of temperature on translocation. Translocation increased with temperature from 5 to 35°C. This represents the cumulative effect of temperature on all the component processes involved in translocation - the transfer of assimilate from the source mesophyll cells to the source sieve tubes, transport through the sieve tubes, and the transfer from the sink sieve tubes to the sink mesophyll cells and the concomitant utilization or compartmentation of the translocate. It can not be determined from these data which of the component processes are limiting or controlling the translocation rate at any particular point. The rate at which available translocate is transferred to the conducting elements of the source is affected by the metabolic status of the source (Giaquinta, 1977; Doman and Geiger, 1979), and the removal of translocate from the conducting elements of the sink is dependent, directly or indirectly, on a supply of metabolic energy (Giaquinta, 1980; Geiger and Fondy, 1980). Therefore, temperature will have a profound effect on both these sets of processes. Transport through the sieve tubes is generally fairly insensitive to temperature over a moderate temperature range, but inhibited at temperature extremes (Swanson and Böhning, 1951; Webb and Gorham, 1965). Bean is a chilling sensitive plant, and chilling a portion of the path to 10°C will cause a severe disruption of translocation (Giaquinta and Geiger, 1973). This would override any effect of temperature on the source or sink.

It is important to realize that any extrapolations from the present data to a field situation must be made with caution for the following reasons:

1. A highly modified plant system, with a relatively low sink:source ratio was used. Plants growing under field conditions would normally have a much higher sink:source ratio.

2. The experiments were conducted with young plants still in a vegetative state. The effect of temperature on translocation may be different in older plants, which are in a reproductive stage of developement.

3. These experiments were short-term. The plants were grown at 20°C and exposed to the experimental temperature only for 3 hours. The effect of temperature on translocation over this short period may be quite different from its effect in the long term. There is some indication that this is the case. While translocation was initially greater at 35 than at 30°C after 3 hours, translocation at 35°C had slowed to a rate less than that at 30°C. Also it has been shown that the optimum temperature for translocation will vary with the growing temperature (Ritcher and Hoddinott, in prepration).

The data presented here indicate the short-term effect of temperature on translocation when the temperature of all the component parts of a single source-single sink translocation system are varied. Further work could involve using plants with a high sink:source ratio, using a higher

light intensity, or using a more complex translocation system.

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